THE FUNCTIONAL MORPHOLOGY OF THE ORGANS OF THE MANTLE CAVITY OF *PERNA VIRIDIS* (LINNAEUS, 1758) (BIVALVIA: MYTILACEA)

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ABSTRACT

In Hong Kong and throughout its large geographic range, the epibyssate mussel *Perna viridis* (Linnaeus) tolerates widely varying hydrographic regimes. Obvious physiological adaptations are matched by appropriate interpopulation variations in life history characteristics.

This study of feeding structures and mechanisms in the mantle cavity reveals other, morphological, adaptations. Ctenidial collection areas are relatively small. Similarly, the sorting areas of the labial palps are small and the dorsal edges of the palps are extensively fused to either the visceral mass or the mantle so that they rigidly project backwards into the mantle cavity and are thus intimately apposed to the ctenidia. The anterior ends of the ctenidia and the sorting areas of the palps are mostly rejectory. Although of the basic mytilid form, the arrangement of the feeding organs, and their ciliary currents, reveals how *Perna viridis* is particularly able to occupy waters with high sediment loadings. The efficiency of particle rejection suggests that high turbidities do not limit the distribution of *P. viridis*. Such adaptations, together with other physiological and reproductive adaptations, account for the dominance of this species in tropical estuarine and other marine environments.

The genus *Perna* is represented by three species having non-overlapping geographic ranges. *P. canaliculus* (Gmelin) is restricted to New Zealand, *P. perna* (Linnaeus) is widely distributed along the coasts of Africa and the Atlantic coasts of South America while *P. viridis* (Linnaeus) is Indo-Pacific (Siddall, 1980). *P. viridis* is widely distributed within the Indo-Pacific, having a western limit at the Persian Gulf and an eastern limit at New Guinea. It has not been recorded south of New Guinea and Habe (1977) considers southern Japan to be its northern limit. Interestingly, Siddall (1980) does not consider *P. viridis* to be naturally distributed along the coast of China or Japan and Arakawa (1980) believes the species was introduced into Japan sometime around 1967. Possibly, therefore, the species has been introduced into Hong Kong also. Irrespective of this, *P. viridis* is a dominant feature of many hard intertidal and subtidal habitats in Hong Kong.

The distribution of *Perna viridis* in Hong Kong waters has been reported upon by Huang *et al.* (1985). Hong Kong can be divided longitudinally into three hydrographic zones (Fig. 1): a western estuarine zone, greatly under the influence of the Pearl River, is characterised by fluctuating low salinities and high sediment loadings; an eastern zone, in which shores are exposed to predominately oceanic waters and a central transition zone where western and eastern waters meet and the water column is stratified (Morton, 1982, 1985).

Transition zone waters are also typical "harbour" waters encompassing two important harbours, Victoria and Tolo. *Perna viridis* can be found throughout Hong Kong's waters, excluded only from areas experiencing extremely low salinities as at Tsim Bei Tsui in Deep Bay in the northwestern quadrant of Hong Kong and from the exposed reaches in the southeastern quadrant of Hong Kong. Figure 1 summarises distribution data and shows that highest densities (>200 adult individuals m^{-2}) are consistently recorded from Victoria and Tolo Harbours. Lower densities (<100 m^{-2}) are recorded from eastern and western waters. Huang *et al.* (1985) explain the local distribution of *P. viridis* by suggesting that the consistently low salinities ($<5^0/_{00}$) in the west and exposure to wave action in the east limit establishment and growth. Lee and Morton (1985) consider that the wide distribution implies successful adaptation to a broad range of hydrographies, but that differences in densities reflect water quality preferences. *P. viridis* is most abundant in Victoria and Tolo Harbours where the water is polluted by domestic, agricultural and industrial effluents (Morton, 1982, 1985). Lee (1985) has shown that in
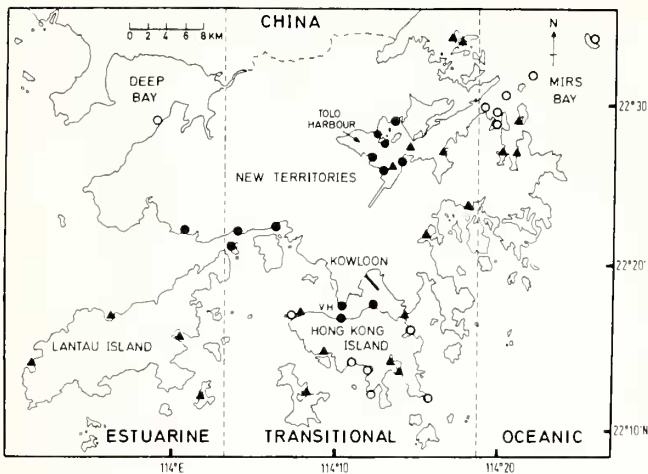
Fig. 1. The distribution of *Perna viridis* in Hong Kong, in relation to broadly recognised hydrographic zones (After Huang *et al.*, 1985) (Solid circles, density > 100 m⁻²; triangles, density < 100 m⁻²; open circles, *P. viridis* not found).

Fig. 2. *Perna viridis*. The animal as seen from the right side and after removal of the right shell valve and mantle lobe. Ciliary currents are indicated by arrows [B, byssus; CT, ctenidium; DD, digestive diverticula; ES, exhalant siphon; F, foot; H, heart; IA, inhalant aperture; K, kidney; PA, posterior adductor muscle; PBR(1) and PRB(2), components of the posterior byssal retractor muscle; RILP, right inner labial palp; ROLP, right outer labial palp].

Fig. 3. *Perna viridis*. The animal as seen from the right side and after removal of the right shell valve, mantle lobe, right ctenidium and right labial palps to show the ciliary currents of the visceral mass [ABR; anterior byssal retractor muscle; B, byssus; CT, ctenidium; DD, digestive diverticula; ES, exhalant siphon; F, foot; H, heart; IA, inhalant aperture; K, kidney; LILP, left inner labial palp; PA, posterior adductor muscle; PBR(1) and PBR(2), components of the posterior byssal retractor muscle].

Victoria Harbour, *P. viridis* shows retarded growth rates, precocious mortality and low tissue weights. Despite these pollution induced stresses, *P. viridis* dominates the epifaunal community by virtue of physiological tolerances and a restricted breeding season. In other parts of Hong Kong, where the species is less numerous, it grows faster, lives longer, has greater tissue weights and breeds year round, so that here too the species is a significant feature of the epifaunal community.

Apart from descriptions of the shell, e.g. Siddall (1980), there is no comprehensive morphological study of *Perna viridis*. This study investigates the functional morphology of the organs of the mantle cavity of *P. viridis*, to determine if there are anatomical and functional characteristics that supplement physiological and life history characteristics permitting the exploitation of a wide range of habitats.

MATERIALS AND METHODS

Specimens of *Perna viridis* were obtained from the pier at Wu Kwai Sha, Tolo Harbour, New Territories of Hong Kong in March 1986. Following dissection, ciliary currents were elucidated using fine grade carborundum and powdered milk. For histological purposes, specimens were fixed in Bouin's fluid, decalcified, sectioned at 6 μm and alternate slides stained in either Ehrlich's haematoxylin and eosin or Masson's trichrome.

FUNCTIONAL MORPHOLOGY

Perna viridis is mytiliform, with extreme reduction of the anterior but expansion of the posterior faces of the shell and ventral flattening (Fig. 2). Although the form of *P. viridis* is not so extreme as open-coast mytilids, e.g. *Septifer* (Yonge
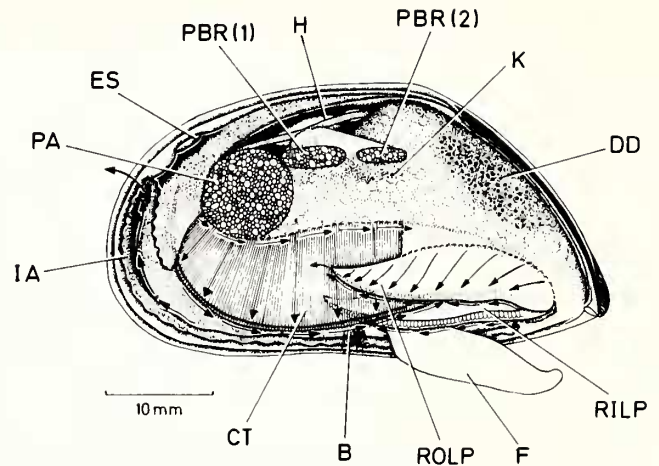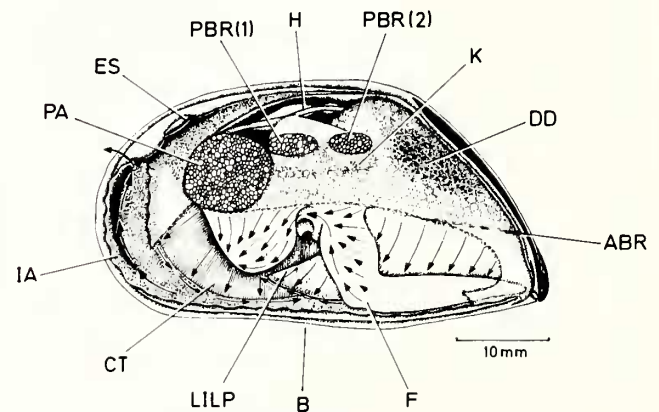
and Campbell, 1968), with ventral flattening such that the greatest shell width is basal, an unusual feature is the absence of an anterior adductor muscle, i.e. *P. viridis* is monomyarian (as are other species of the genus). The posterior adductor muscle is large (Fig. 2: PA), as is the posterior byssal retractor muscle which is divided into two components [PBR (1), PBR(2)]. The anterior byssal retractor (Fig. 3: ABR) is small and located posterior to the umbones, below the ligament.

THE MANTLE

Mantle fusion only occurs between the inhalant and exhalant apertures. The latter is conical (Figs. 2, 3: ES), the former (IA) long and without the sensory papillae typical of other mytilids, e.g. *Mytilus* (Soot-Ryen, 1955) and *Xenostrobus* (Wilson, 1979). The mantle is variably patterned dark brown, but usually with a darker stripe decorating each side of the outer surface of the exhalant siphon and the inner surfaces of the inhalant aperture. The mantle contains much of the gonad and the ventral mantle margin, seen in transverse section in Figure 4, comprises the usual three folds (Yonge, 1957, 1982): inner (IMF), middle (MMF) and outer (OMF). The outer and middle folds are of the typical plan and fulfill typical functions (Yonge, 1983). Of interest, however, is the inner fold which is greatly enlarged and divided into two components; inner [IMF(I)] and outer [IMF(O)]. The inner component has an extensive haemocoel and probably can be inflated with blood. Between it and the general mantle surface is a deep, densely ciliated, rejectory tract (RT). The outer component of this fold is secretory and possesses a large sub-epithelial gland (MG), the basiphilic cells of which are some 20 μm in diameter. It is believed that these glands, along with other glands in the foot (not illustrated), produce the copius amounts of mucus that are characteristic of *Perna viridis*.
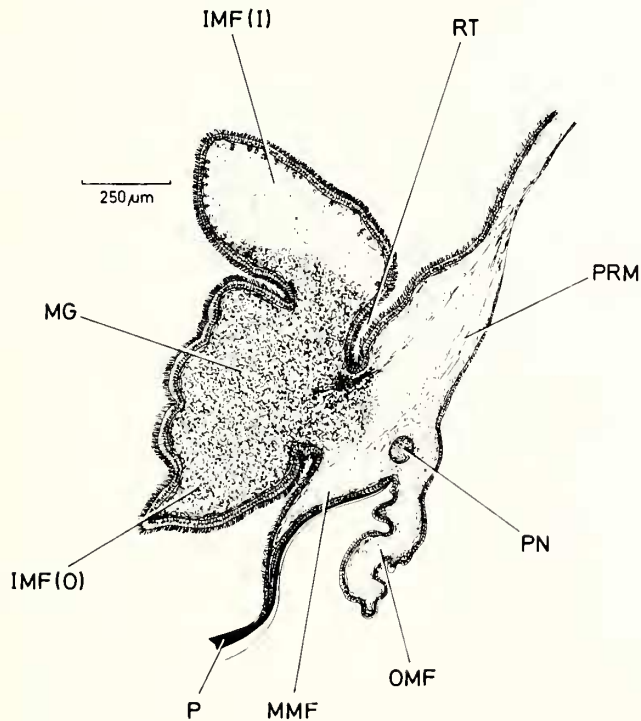
THE CTENIDIA

Unlike the majority of bivalves where the larger proportion of the mantle cavity is located lateral to the visceral mass, that of the Mytilacea, including *Perna viridis*, is largely beneath the body in the expanded ventral component of the shell.

The ctenidia are generally typical of the Mytilacea and are flat, homorhabdic, non-plicate, filibranch and comprise approximately equal inner and outer demibranchs (Figs. 2, 3). The gill ciliation is of type B(1) (Atkins, 1937). The ctenidia are removed from the anteriormost apex of the shell and the anterior filaments of the ctenidia are unusually arranged. In the boring mytilid *Adula falcata* (Gould), Fankboner (1971) showed that the outer demibranchs are typically some 10 filaments shorter at their anterior ends than the inner demibranchs. Material arriving at the ctenidial-labial palp terminus on the outer demibranch, therefore, must pass onto the inner demibranch before proceeding to the palps and mouth. Similar situations exist in other mytilids, e.g. *Limnoperna, Musculista, Modiolus* and *Arcuatula* (Morton, 1973, 1974, 1977a, b, 1980). This is not the case in *Perna viridis*. Anteriorly (Figs. 5, 6), the demibranchs (ID; OD) are of the same length, but particles arriving at the terminus in the ventral margin food groove of the outer demibranchs stop about 14 filaments from the end. Moreover, the cilia in the ventral marginal food groove of the anteriormost 14 filaments, beat posteriorly so that the two streams meet and from this point (Figs. 5, 6: star) transported particles can fall onto the palps (RILP, ROLP) for resorting.
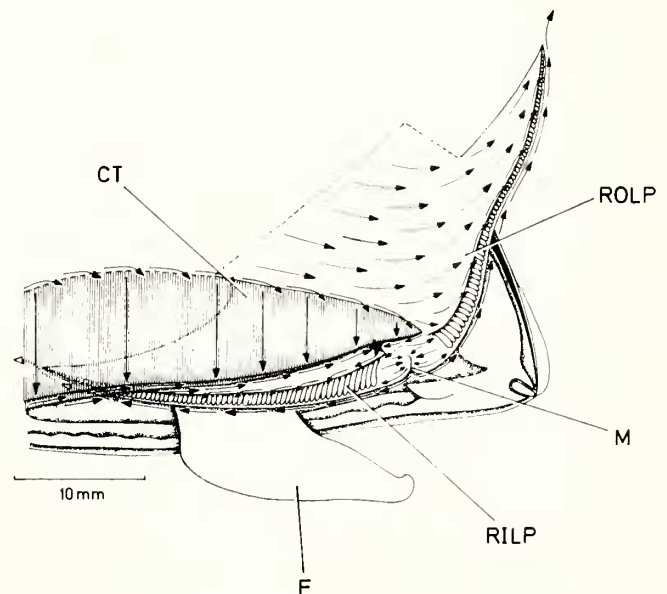

Fig. 4. *Perna viridis.* A transverse section through the right mantle margin at the pedal gape and showing the extent of the mucous gland (MG) in the outer component of the inner mantle fold [IMF(O)], [IMF(1), IMF(2), inner and outer components of the inner mantle fold; MG, mucous gland; MMF, middle mantle fold; OMF, outer mantle fold; P, periostracum; PN, pallial nerve; PRM, pallial retractor muscle; RT, rejectory tract].

Fig. 5. *Perna viridis.* A detail of the anterior region of the body, after removal of the right shell valve and mantle lobe and showing the ciliary currents of the anterior half of the ctenidium and palps in greater detail. The star identifies where ctenidially collected particles fall onto the palps (CT, ctenidium; F, foot; M, mouth; RILP, right inner labial palp; ROLP, right outer labial palp).
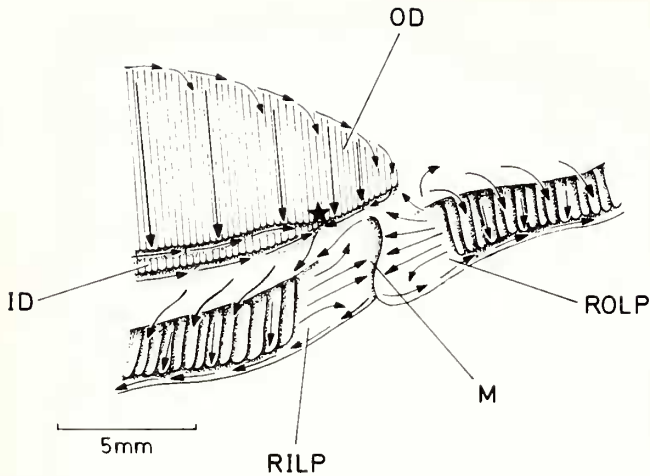
Fig. 6. *Perna viridis*. A further detail of the anterior region of the ctenidium and labial palps showing the ciliary currents. The star identifies where ctenidially collected particles fall onto the palps (ID, inner demibranch; M, mouth; OD, outer demibranch; RILP, right inner labial palp; ROLP, right outer labial palp).
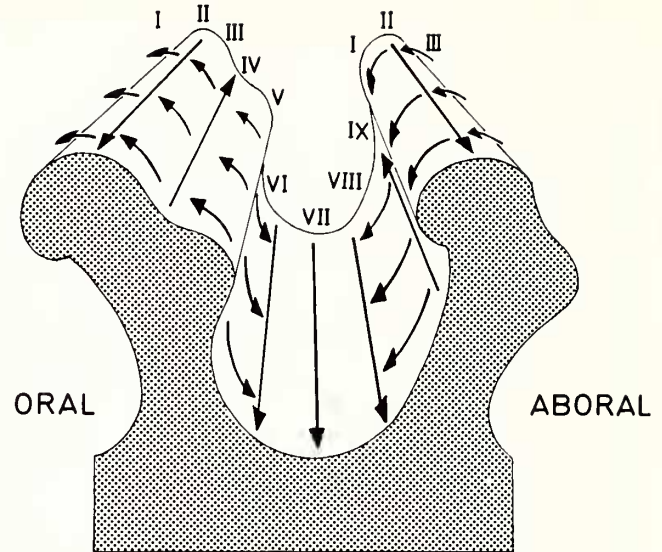

Fig. 7. *Perna viridis*. A diagrammatic representation of two ridges of a labial palp to show the various ciliary tracts [For explanation of Roman numerals see text, but note that there is no powerful acceptance tract sweeping particles over the palp crests as in other mytilids, e.g. *Modiolus metacalfei* Hanley (Morton, 1977a: Fig. 8)].

THE LABIAL PALPS

The unusual ctenidial terminus of *Perna viridis* is matched by equally unusual palps. As might be expected from an inhabitant of turbid waters, the labial palps are both large and long (Fig. 2: RILP, ROLP), reaching backwards for some half of the length of the mantle cavity. Unlike other bivalves, especially other mytilids, however, the dorsal edges of the palps are united with either the mantle or the visceral mass, for more than two-thirds of their lengths. In the case of the outer demibranch, union is with a flap of the mantle (Fig. 2), while in the case of the inner palps, union is with the visceral mass at a point just below where the palp attaches to the ascending lamella of the inner demibranch (Fig. 5). In addition, the sorting area of each palp is small, restricted to a thin line of ridges along the inner ventral margin (Figs. 5, 6). The large naked surfaces of the inner and outer faces of both inner and outer palps bear strong ciliary currents which pass material downwards and backwards towards the tips of the palps. Some of this material passes onto the filaments of the inner ventral margin of the palp, but the great majority quickly flows over the ridges to the ventral edge where a strong rejectory tract also passes this to the palp tips. The great majority of material arriving at the ctenidial terminus is therefore quickly rejected.

The ciliary currents of the palp ridges have been examined in detail (Fig. 7). In the grooves between each ridge, material is passed downwards (VI, VIII) to contribute to a major rejectory tract in the depths of the grooves (VII). The crests of the grooves are characterised by acceptance and resorting currents. Passing orally over the crests of the palps are extraordinarily weak acceptance tracts (I, III). In fact, unlike the majority of bivalves where the acceptance tracts are powerful, creating a major flow, it is difficult to discern such currents in *Perna viridis*. Also on the crests of each ridge is

a resorting current (II) passing material towards the ventral edge of the palp. On the oral face of each ridge are cilia transporting material down into the groove (I), while on the aboral face, opposing currents (III, V) take material out of the groove. On both faces are longitudinal resorting currents (IV, IX), transporting material dorsally, away from the ventral rejectory tract.

The palp ridges, therefore, are of typical mytilid form, possessing an array of acceptance, resorting and rejection tracts. The first of these functions is, however, severely reduced and the palps largely fulfill a rejectory or cleansing role.

THE FOOT AND CILIARY CURRENTS OF THE VISCERAL MASS AND MANTLE.

The foot (Figs. 2, 3: F) is of the typical mytilid form, long, highly mobile and plantar. At rest, it projects into the anteriormost reaches of the mantle cavity, a small hook-like distal swelling positioning it behind the anterior lip of the mouth (Fig. 3).

The foot, as in most bivalves, bears few ciliary tracts. The dorsal regions of the foot and the visceral mass, however, bear powerful ciliary currents which pass material postero-dorsally and then postero-ventrally to the posterior edge of the visceral mass where the material falls onto the mantle below (Fig. 3).

The ciliary currents of the mantle are similarly rejectory. On the general surface of the mantle, material is passed downwards and backwards on each lobe to accumulate in a deep posteriorly directed, rejection tract (Fig. 4: RT), on the inner mantle margin. Such material, in the form of a

mucus-bound pseudofaecal string, is passed posteriorly towards the inhalant aperture. Here such material is passed dorsally and is eventually rejected from the dorsal edge of the inhalant aperture (Figs. 2, 3) as is typical of the Mytilacea (Morton, 1973).

DISCUSSION

Throughout its broad range, *Perna viridis* has been reported to have a phenomenal growth rate of some 10 mm per month, so that a marketable size of rope-cultured individuals is achieved within six months. Comparative growth rates for Goa, Johore Straits, the Philippines and Penang are 8, 10, 9 and 10 mm per month, respectively (Choo, 1974; Rao et al., 1975; Qasim et al., 1977; Cheong and Chen, 1980; Walker, 1982).

In waters of different quality, *Perna viridis* either exhibits continuous breeding and spat recruitment, as in the Johore Straits (Tham et al., 1973; Choo, 1974) and Quezon, Philippines (Walter, 1982), or reproduction centres around two peaks in March-April and October-November (Rao et al., 1975; Sivalingham, 1977). The differences in water quality which are responsible for such a reproductive dichotomy also expose the animal to different physiological stresses. *P. viridis*, like its European counterpart, *Mytilus edulis* (Linnaeus), appears to be generally adapted to the variable physiochemical environment of the low intertidal of estuaries (and harbours) (Davenport, 1983). This author has demonstrated that *P. viridis* has a greater tolerance of reduced salinities than *M. edulis* and that ciliary rates of *P. viridis* are maximal between temperatures of 32-36°C, as compared with 25-32°C for *M. edulis*. *P. viridis* is also capable of surviving prolonged emersion by aerial respiration which *M. edulis* does not (Davenport, 1983). Importantly, *P. viridis* tolerates very high turbidities in locations where it is most abundant, i.e. the Straits of Johore (Cheong and Chen, 1980), Penang, Malaysia (Choo, 1974), the Ennore estuary, Madras (Shafee, 1979), Thailand (Chonchuenchob et al., 1981) and Hong Kong (Huang et al., 1985; Lee, 1985; Lee and Morton, 1985).

With such growth rates, high fecundity and physiological tolerance to fluctuating estuarine environments, it seemed to this author that *P. viridis* could possess unusual morphological adaptations that allow it to cope with particularly high sediment loads. On the basis of the above observations it is clear that nutrient supply to *P. viridis* is unlikely to be limiting and that the animal is more likely to be morphologically adapted to removing sediment. This is so, but importantly, the adaptations are different from those possessed by deposit feeding bivalves of soft muds. In the infaunal Tellinacea, for example, the ctenidia are typically small, while the palps and their sorting ridges are respectively large and extensive (Yonge, 1949). Similarly in members of the Solenacea, e.g. *Sinonovacula* (Morton, 1984) and *Orbicularia* (Purchon, 1984), the same generalisation holds true. On the other hand, the mangrove anomiid, *Enigmonia aenigmatica* (Holton), though living in highly turbid waters such as the Straits of Johore, where *P. viridis* also occurs, has small labial

palps with ciliary tracts that are wholly acceptance oriented. Sorting, in addition to collection, is effectively the role of the ctenidia (Morton, 1976). Clearly different bivalves have different ways of handling highly turbid inhalant water.

For the Mytilidae, ctenidia and palp structure and size have been considered to be relatively uniform (Fankboner, 1971). The ctenidia are ventral, as opposed to lateral, in position and the palps long and strap-like and divided into two components: a dorsal unridged area and a ventral region of strong ridging, e.g. *Septifer* (Yonge and Campbell, 1968), *Adula* (Fankboner, 1971), *Limnoperna, Musculista, Modiolus* and *Arcuatula* (Morton, 1973, 1974, 1977a, b, 1980). In addition, the anterior extent of the outer demibranch is shorter than that of the inner, the ctenidial-labial palp junction being diagnostic for the family (Fankboner, 1971). These generalisations are not so applicable to *Perna viridis*. Both demibranchs are of equal length, but with transport of material along the food grooves to a point about 14 filaments from the anterior end of the ctenidium. Anterior to this, particles move posteriorly along the food grooves to this point. Similarly, although the palps are relatively enormous, they have only a small ventral sorting area and further that although an usual array of acceptance, resorting and rejection tracts on the ridges and grooves are present, the acceptance tracts are so weak as to be just detectable. Moreover, by fusion with the mantle and visceral mass, the palps are not freely mobile as in other bivalves, but firmly project backwards into the mantle cavity, enforcing apposition with the ctenidia. *P. viridis* also secretes copious amounts of mucus from extensive glands within the foot and along the entire length of the mantle margin contained within a specialised sub-fold of the inner mantle fold. Finally, there are strong rejectory tracts in the mantle margins and on the visceral mass.

The organs of the mantle cavity of *P. viridis* are adapted for the rejection of considerable quantities of sediment. Material in the inhalant water is thickly bound up with mucus and, in the anterior regions of the mantle cavity, virtually all surfaces are concerned with rejection of these mucus-bound strings of particulate material. Probably only the finest particles are accepted. The adaptations shown by *P. viridis* are wholly different from those of other bivalves inhabiting turbid waters and, moreover, represent a significant deviation from the standard mytilid plan. Common mytilid features, such as the ventral mantle cavity, strap-like palps and dorso-ventrally narrow ctenidia relate to the evolution of the heteromyarian form (*P. viridis* is, however, monomyarian), particularly in connection with the reduction of the anterior component of the mantle cavity. The peculiar adaptations noted above, however, clearly relate to the success of *P. viridis* in turbid tropical estuarine waters and complement physiological and reproductive adaptations.

LITERATURE CITED

Arakawa, K. Y. 1980. On alien immigration of marine sessile invertebrates into Japanese water. *Marine Fouling* 2:29-39.

Atkins, D. 1937. On the ciliary mechanisms and interrelationships

of lamelllibranchs. Part 3. Types of lamellibranch gills and their food currents. *Quarterly Journal of Microscopical Science* 79:375-421.

Cheong, L. and F. Y. Chen. 1980. Preliminary studies on raft method of culturing green mussels, *Perna viridis* (L.), in Singapore. *Singapore Journal of Primary Industry* 8:119-133.

Chonchuenchob, P., Chalayondeja, K. and K. Mutarasint. 1981. Hanging culture of the green mussel (*Mytiluls smaragdinus* Chemnitz) in Thailand. *ICLARM Translations* 1:1-14.

Choo, P. S. 1974. Preliminary studies on culture of the mussel, *Mytilus viridis*, Linnaeus (Mollusca, Mytilidae) in Penang. *The Malaysian Agricultural Journal* 49:514-524.

Davenport, J. 1983. A comparison of some aspects of the behaviour and physiology of the Indian mussel *Perna (= Mytilus) viridis* and the common mussel *Mytilis edulis* L. *Journal of Molluscan Studies* 49:21-26.

Fankboner, P. V. 1971. The ciliary currents associated with feeding, digestion, and sediment removal in *Adula (Botula) falcata* Gould 1851. *Biological Bulletin* 140:28-45.

Habe, T. 1977. *Systematics of Mollusca in Japan. Bivalvia and Scaphopoda.* Hokuryukan Publishing Co. Ltd., Tokyo, Japan 372 pp.

Huang, Z. G., Lee, S. Y. and P. M. S. Mak. 1985. The distribution and population structure of *Perna viridis* (Bivalvia:Mytilacea) in Hong Kong waters. *In: Proceedings of the Second International Workshop on the Malacofauna of Hong Kong and southern China, Hong Kong, 1983.* B. Morton and D. Dudgeon, eds. pp. 465-471. Hong Kong University Press, Hong Kong.

Lee, S. Y. 1985. The population dynamics of the green mussel, *Perna viridis* (L.) in Victoria Harbour, Hong Kong - dominance in a polluted environment. *Asian Marine Biology* 2:107-118.

Lee, S. Y. and B. Morton. 1985. The Hong Kong Mytilidae. *In: Proceedings of the Second International Workshop on the Malacofauna of Hong Kong and southern China, Hong Kong, 1983.* B. Morton and D. Dudgeon, eds. pp. 49-76. Hong Kong University Press, Hong Kong.

Morton, B. 1973. Some aspects of the biology and functional morphology of the organs of feeding and digestion of *Limnoperna fortunei* (Dunker) (Bivalvia:Mytilacea). *Malacologia* 12:265-281.

Morton, B. 1974. Some aspects of the biology, population dynamics and functional morphology of *Musculista senhausia* Benson (Bivalvia:Mytilacea). *Pacific Science* 28:19-33.

Morton, B. 1976. The biology, ecology and functional aspects of the organs of feeding and digestion of the S.E. Asian mangrove bivalve, *Enigmonia aenigmatica* (Mollusca:Anomiacea). *Journal of Zoology (London)* 179:437-466.

Morton, B. 1977a. The biology and functional morphology of *Modiolus metcalfei* Hanley 1844 (Bivalvia:Mytilacea) from the Singapore mangrove. *Malacologia* 16:500-518.

Morton, B. 1977b. An estuarine bivalve (*Modiolus striatulus*) fouling raw water supply systems in West Bengal, India. *Journal of the Institute of Water Engineers and Scientists* 31:441-452.

Morton, B. 1980. The biology and some aspects of the functional morphology of *Arcuatula elegans* (Mytilacea:Crenellinae). *In: Proceedings of the First International Workshop on the Malacofauna of Hong Kong and southern China, Hong Kong, 1977.* B. Morton, ed. pp. 331-345. Hong Kong University Press, Hong Kong.

Morton, B. 1982. An introduction to Hong Kong's marine environment with special reference to the north-eastern New Territories. *In: Proceedings of the First International Marine Biological Workshop: The Marine Flora and Fauna of Hong Kong and southern China, Hong Kong, 1980.* B. Morton and C. K. Tseng, eds. pp. 25-53. Hong Kong University Press, Hong Kong.

Morton, B. 1984. The functional morphology of *Sinonovacula constricta* with a discussion on the taxonomic status of the Novaculininae (Bivalvia). *Journal of Zoology (London)* 202:299-325.

Morton, B. 1985. Marine pollution induced environmental changes in Hong Kong - the Tolo Harbour case study. *In: Pollution in the Urban Environment, Polmet '85, Hong Kong.* M. H. W. Chan, R. W. M. Hoare, P. R. Holmes, R. J. S. Law and S. B. Reed, eds. pp. 548-558. Elsevier Applied Science Publishers, London and New York.

Purchon, R. D. 1984. The biology of *Orbicularia orbicularia* (Bivalvia:Tellinacea). *Asian Marine Biology* 1:27-48.

Qasim, S. Z., Parulekar, A. P., Harkantra, S. N., Ansari, Z. A. and A. Nair. 1977. Aquaculture of green mussel *Mytilis viridis* L.: cultivation on ropes from floating rafts. *Indian Journal of Marine Science* 6:15-25.

Roa, K. V., Kumari, L. K. and S. N. Dwiveri. 1975. Biology of the green mussel, *Mytilus viridis.* *Indian Journal of Marine Science* 4:189-197.

Shafee, M. S. 1979. Ecological energy requirements of the green mussel, *Perna viridis* Linnaeus from Ennore Estuary, Madras. *Oceanologia Acta* 2:69-74.

Siddall, S. E. 1980. A clarification of the genus *Perna.* *Bulletin of Marine Science* 30:858-870.

Sivalingham, P. M. 1977. Aquaculture of the green mussel, *Mytilus viridis* Linnaeus, in Malaysia. *Aquaculture* 11:297-312.

Soot-Ryen, T. 1955. A report on the family Mytilidae. *Report of the Allan Hancock Pacific Expeditions* 20:1-175.

Tham, A. K., Yang, S. L. and W. H. Tan. 1973. Experiments in coastal aquaculture in Singapore. *In: Coastal Aquaculture in the Indo-Pacific Region.* T. V. R. Pillay, ed. pp. 375-383. Fishing News (Books), Farnham, Surrey, U. K.

Walter, C. 1982. Reproduction and growth in the tropical mussel *Perna viridis.* (Bivalvia:Mytilidae). *Kalikasan, Philippine Journal of Biology* 11:83-97.

Wilson, B. R. 1979. A new generic name for three recent and one fossil species of Mytilidae (Mollusca:Bivalvia) in Southern Australia with redescriptions of the species. *Proceedings of the Malacological Society of London* 37:279-295.

Yonge, C. M. 1949. On the structure and adaptations of the Tellinacea, deposit-feeding Eulamellibranchia. *Philosophical Transactions of the Royal Society* (Series B) 234:29-76.

Yonge, C. M. 1957. Mantle fusion in the Lamellibranchia. *Publicazioni della Stazione Zoologica di Napoli* 29:151-171.

Yonge, C. M. 1982. Mantle margins with a revision of siphonal types in the Bivalvia. *Journal of Molluscan Studies* 48:102-103.

Yonge, C. M. 1983. Symmetries and the role of the mantle margins in the bivalve Mollusca. *Malacological Review* 16:1-10.

Yonge, C. M. and J. I. Campbell. 1968. On the heteromyarian conditions in the Bivalvia with special reference to *Dreissena polymorpha* and certain Mytilacea. *Transactions of the Royal Society of Edinburgh* 68:21-43.